

# A NEW MULTIPLE-FLOATED *AZOLLA* FROM THE EOCENE OF BRITAIN WITH A BRIEF REVIEW OF THE GENUS

by M. E. COLLINSON

**ABSTRACT.** Megaspores and microspore massulae of *Azolla cobwellensis* sp. nov. are described from the Upper Eocene, Upper Headon Beds of Colwell Bay, Isle of Wight. The megaspores possess a multifloated 'swim apparatus' with three tiers of floats. The floats are arranged in three groups of six. There is a distinct collar at the junction with the megaspore zone and hairs arising from this collar enmesh the floats. The microspore massulae possess occasionally septate, grapnel-tipped glochidia. This species is the youngest multifloated *Azolla* yet recorded and is the only multifloated species which possesses a collar. It further supports recent hypotheses that a number of lines of evolution have been involved in the development of extant *Azolla* species. A review of the sixty species recorded in the genus *Azolla* is presented in the form of a table showing stratigraphic ranges and features of the megaspores and massulae. Certain species are discussed in detail with relation to the morphology of *A. cobwellensis*.

THE material here described was collected from folded strata of the Upper Headon Beds at the northern end of Colwell Bay, Isle of Wight (these beds are indicated on the section Pl. V in Keeping and Tawney 1881 and p. 103). The horizon sampled was 1.5 m from the cliff base at Linstone Chine (N.G.R. SZ 33058862), and comprised a purplish-black homogeneous silty clay.

Plant remains from the Upper Headon Beds in Colwell Bay have been described by Chandler (1963). Stratigraphically these beds have been considered either as Upper Eocene or Lower Oligocene in age. A discussion of this controversy may be found in Curry *et al.* (1978). I follow these authors and Cooper (1976) in regarding these beds as Upper Eocene in age with the Eocene/Oligocene boundary at the base of the Bembridge Marls.

## MATERIAL AND METHODS

The sample was disaggregated using hydrogen peroxide solution and separated into size fractions by sieving (Collinson 1978*a, b*). No faunal remains were recovered but the sample was rich in pyritic debris. Two macroplant species were present; the first a new species of a *Typha* seed (Collinson 1978*b*) and the second the *Azolla* which forms the subject of this paper. The sieved fractions were treated in hydrofluoric acid to remove unwanted mineral matrix. Specimens for SEM study were allowed to dry in air, mounted on stubs using durofix on a coverglass, and examined under Cambridge S 600, Mark IIA and S 180 scanning electron microscopes. Specimens studied with transmitted light were cleared using Schultze's solution for up to one hour and mounted in glycerine jelly. Transmitted and reflected light micrographs were taken using a Zeiss photomicroscope.

## SYSTEMATIC DESCRIPTION

Family SALVINIACEAE Dumortier

Genus *AZOLLA* Lamarck

Section FLORSCHUTZIA Kempf, 1968

(= KREMASTOSPORIA Jain and Hall, 1969)

*Azolla cobwellensis* sp. nov.

Plate 23, figs. 1-4, 7; Plate 24, figs. 1-9; text-fig. 1*a-e*

*Syntypes.* Plate 23, fig. 1 V59717a; Plate 23, fig. 7 V59718; Plate 24, fig. 7 V59717d; Plate 23, fig. 4 V59719. V numbers refer to catalogue numbers in the Palaeontology Department, British Museum (Natural History) London, where all the figured material has been deposited. Additional unfigured material has also been deposited, V59722.

*Type locality.* Linstone Chine (SZ 33058862) Colwell Bay, Isle of Wight, England.

*Type horizon.* Upper Headon Beds.

*Diagnosis.* Megaspore apparatus with eighteen (up to twenty-four) floats arranged in three tiers. Float zone of greater extent than megaspore zone and delimited by an apical cap and a basal collar at the junction with the megaspore. Total length 377–550  $\mu\text{m}$ . Breadth (widest) 180–462  $\mu\text{m}$ . Surface of floats sparsely hairy (supraflosom *sensu* Fowler and Stennett-Willson, 1978), hairs originating from the collar. Exoperine columnar–rugulate obscured by infraflosom derived from the rugulae. Endoperine granular pierced by small foveolae. Exine surface granular, total wall thickness 14–24  $\mu\text{m}$ . Microspore massulae circular or elliptic (120  $\times$  120–180  $\times$  140  $\mu\text{m}$  in diameter), attached to megaspores and also dispersed. Microspores at least eight per massula, trilete, subglobular–subcircular, 14–20  $\mu\text{m}$  in diameter. Laesurae extending two-thirds of their radius. Glochidia with dilation and constriction below an anchor-shaped tip with recurved hooks. Occasional glochidia septate, with one or two distally placed septae.

*Description.* Megaspore apparatus with eighteen floats, closely packed and arranged in three tiers. Floats of the lower tier are often subdivided into two, one of which is very small, yielding a potential total of twenty-seven floats per megaspore although no more than twenty-four have been counted on the available material. The floats of the upper tiers are larger than those of the lower tier and they are quadrangular–hexagonal in surface shape (Pl. 23, figs. 1, 4). The float zone is larger than the megaspore zone (Pl. 23, fig. 7) and is delimited by a truncate apex with an apical cap (Pl. 23, figs. 1, 2; Pl. 24, fig. 2), and by a collar at the junction with the megaspore (Pl. 23, figs. 1, 4; Pl. 24, fig. 5).

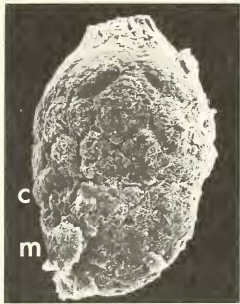
The eighteen floats are arranged in three groups of six (text-fig. 1*d*), each group with one large upper, two smaller middle, and three smallest lower floats (fifteen specimens were available in which the exact number and arrangement of floats was clearly visible). The syntype V59719 (Pl. 23, fig. 4*a–d*), shows this arrangement but also reveals the erroneous impression which can be gained by certain views of the specimen. When compression has obscured all but two flattened faces (e.g. the apparent view of Pl. 23, fig. 4*c*), it appears that there are only twelve to fourteen floats per specimen, six to seven on each flattened face. Alternatively as in Plate 23, fig. 2 and Plate 23, fig. 4*a* there may appear to be only four floats per flattened face.

The collar is visible externally below the lowest tier of floats (Pl. 23, figs. 1, 4) and is partly composed of intertwined hairs (supraflosom) (Pl. 24, fig. 5), which are continued into the central region of the float zone (text-fig. 1*a*) and on to the surface of the floats (Pl. 24, fig. 5 *left*) thus emmeshing them. On the collar, the supraflosom originating in the collar and the infraflosom originating from the megaspore exoperine, are intertwined.

#### EXPLANATION OF PLATE 23

Figs. 1–4, 7. *Azolla colwellensis* sp. nov. Upper Headon beds, Colwell Bay, Isle of Wight. 1, megaspore, syntype, V59717a, showing external appearance of the three tiers of floats, the basal collar (c) and an attached massula (m), SEM,  $\times$  130. 2, megaspore, V59720, showing less well-defined view of floats, comparable with that in fig. 4*a*. Note also hairy exoperine and truncate apical cap, SEM,  $\times$  130. 3, razor-cut vertical section through a megaspore V59717b. Five floats have been sectioned, two on the right, three on the left. The pseudovacuolate collar appears at the base of the float zone and the hairy central column is visible. Damage in the megaspore wall is due to pyrite crystals, SEM,  $\times$  130. 4*a–d*, megaspore, syntype, V59719, showing the float system as viewed in reflected light, rotated through a series of 90° angles. Note the sharp junction between two groups of six floats in 4*a*, and the irregular boundary in 4*c* (right edge). The collar (c) also stands out, being of similar texture to the floats, RLM,  $\times$  125. 7, megaspore, syntype, V59718, showing the proportions of the megaspore and float zone, TLM,  $\times$  100.

Figs. 5, 6. *A. schopfii* Dijkstra, Palaeocene, Slim Buttes, Texas. 5, megaspore showing trilete mark, oval shape, and large foveolae in megaspore wall unobscured by hairs, TLM,  $\times$  100. 6, another megaspore showing the loose arrangement of the floats and the rounded shape, TLM,  $\times$  100.



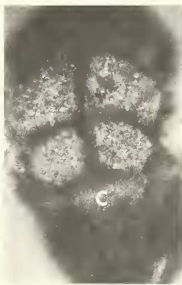
1



2



3



4a



4b



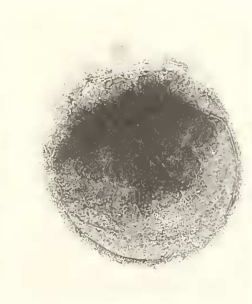
4c



4d



5



6



7

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The floats themselves are distinctly pseudovacuolate structures which extend inwards to the hairy central region (Pl. 23, fig. 3; Pl. 24, fig. 1; text-fig. 1a). These hairs extend in an umbrella-like expansion over the surface of the floats thus enmeshing them and acting as a retention mechanism.

Total length of megaspore apparatus 377–550  $\mu\text{m}$  (mean 437  $\mu\text{m}$ ), breadth 180–462  $\mu\text{m}$  (mean 325  $\mu\text{m}$ ). Length of float zone 200–350  $\mu\text{m}$ , length of megaspore zone 125–240  $\mu\text{m}$  (fifty specimens measured). Upper part of megaspore partly covered by the collar and lower tier of floats, trilete mark not visible. The megaspore is densely hairy externally (Pl. 24, fig. 4) and the perine is divisible into two zones when seen in sectional view. The exoperine is columnar–rugulate and obscured in surface view by intertwined hairs (infrafilosum) arising from the tips of these rugulae (Pl. 24, fig. 3; text-fig. 1b). The endoperine is granular, pierced by small foveolae, variable in thickness, and with foveolae extending to form the pseudovacuolate part of the collar (Pl. 24, fig. 6). Exine surface also granular, exine 3–5  $\mu\text{m}$  thick. Total megaspore wall thickness from 14–24  $\mu\text{m}$ .

Microspore massulae (Pl. 24, fig. 7) circular or elliptic, frequently aggregated in groups of four or eight. Eight megaspores seen with massulae attached. Number of microspores greater than eight but not clearly discernible. Microspores trilete, subtriangular–subglobular (Pl. 24, fig. 8; text-fig. 1c). Glochidia (Pl. 24, fig. 9; text-fig. 1e) 40–50  $\mu\text{m}$  in length, of almost equal width throughout their length but with a prominent dilation and constriction immediately below the tip. Tip anchor shaped with recurved hooks (Pl. 24, fig. 9). Occasional glochidia septate with one or two distal septae (Pl. 24, fig. 8; text-fig. 1e). A single massula may possess both septate and non-septate glochidia.

## FEATURES OF SYSTEMATIC SIGNIFICANCE

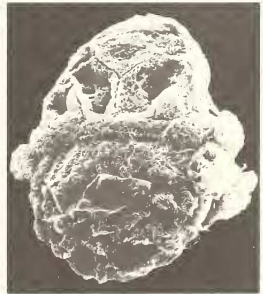
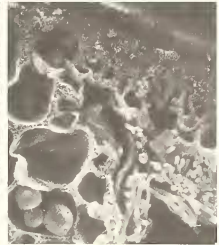
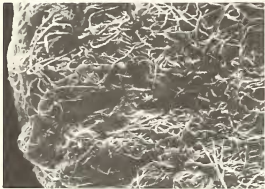
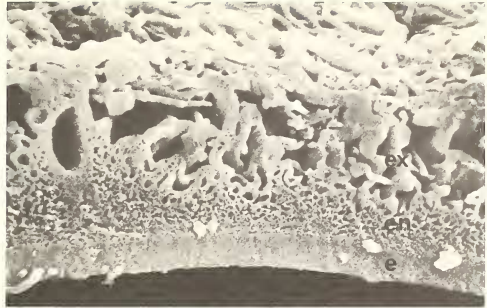
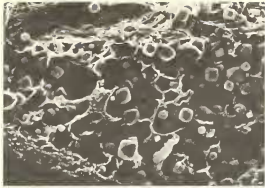
### *Float number and arrangement*

The systematics of *Azolla* species has been characteristically based on the number of floats in the megaspore apparatus. Three, nine, or more (fifteen to twenty-four) represent the three main categories (Hall 1969a). Snead (1969) remarked upon the problem of floats not always being easily distinguishable, and advocated, as did Kempf (1969b), the use of megaspore wall and perispore structure in systematic studies. Snead had, however, attempted to study and illustrate all of his species by transmitted light microscopy. Hall and Swanson (1968) showed how in *A. montana* Hall and Swanson emend. Jain and Hall, 1969 the individual floats are indistinguishable in transmitted light, as they are in *A. colwellensis* (Pl. 23, fig. 7). They can be well displayed using reflected light with a dark background (Pl. 23, fig. 4).

Table 1 lists all the known *Azolla* species and shows that many possess numerous floats in the megaspore apparatus. A number of these are categorized as N or (N). These have numerous floats

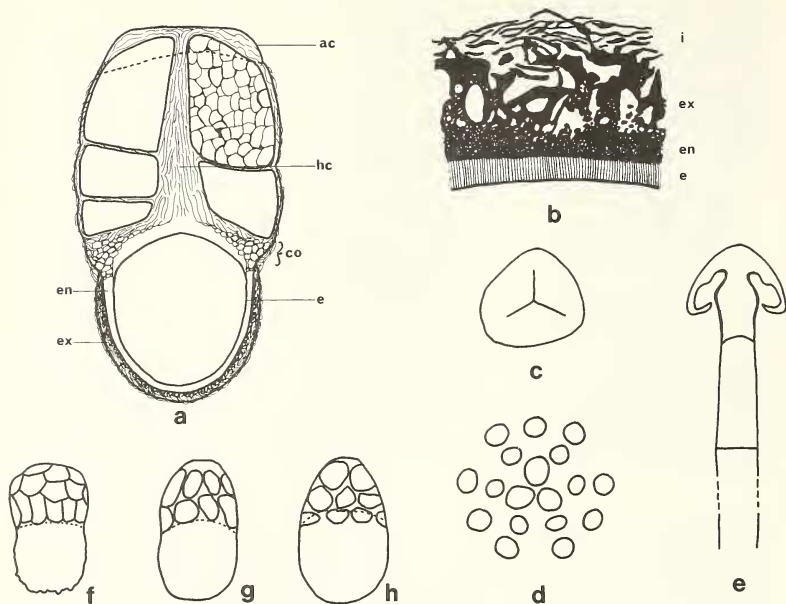
## EXPLANATION OF PLATE 24

- Figs. 1–9. *Azolla colwellensis* sp. nov., Upper Headon Beds, Colwell Bay, Isle of Wight. 1, detail of section in Plate 23, fig. 3 showing pseudovacuolate nature of the floats and hairy central column (upper edge of figure). Note the abundance of pyrite crystals, SEM,  $\times 500$ . 2, detail of the apical cap from Plate 23, fig. 1, SEM,  $\times 150$ . 3, detail of the megaspore wall, V59717c, showing the exine (e), endoperine (en), and exoperine (ex); cf. text-fig. 1b, SEM,  $\times 1750$ . 4, detail of the hairy surface of the megaspore in Plate 23, fig. 1, SEM,  $\times 500$ . 5, detail of the collar surface with float zone to left, from Plate 23, fig. 1, SEM,  $\times 500$ . 6, detail of section through the collar zone at the junction between the collar (left) and megaspore (right). Note the merging of the supra and infra filosal hairs, and the extension of the endoperine to form the pseudovacuolate collar, SEM,  $\times 1000$ . 7, a single massula from a cluster, syntype, V59717d, SEM,  $\times 800$ . 8, detail of a fragment of a massula, V59721, showing a trilete microspore (m) and septate glochidia with anchor-shaped tips, TLM,  $\times 1000$ . 9, detail of the tip of a glochidium, SEM,  $\times 3500$ .
- Figs. 10–12. *A. prisca* Reid and Chandler emend. Fowler, 1975. 10, specimen of typical form from the Bembridge Marls, Hamstead Ledge, Isle of Wight, V60110. Note three floats and massulae aggregated around the collar, SEM,  $\times 125$ . 11, specimen from the Lower Headon Beds (Unio Band) of Hordle, Hampshire, V60111, a new record for this species, SEM,  $\times 125$ . 12, an atypical specimen from the Bembridge Marls of Hamstead Ledge showing septation of the lower tier of floats, V60112, SEM,  $\times 125$ .



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TEXT-FIG. 1a-e. Features of *Azolla cobwellensis* sp. nov., Upper Headon Beds, Colwell Bay, Isle of Wight. a, longitudinal section of the megaspore apparatus,  $\times 150$ . b, section showing the megaspore wall stratification,  $\times 1000$ . c, microspore,  $\times 1000$ . d, diagrammatic, expanded apical view of the float distribution. e, detail of the gnapnel tip of a glochidium,  $\times 3000$ . f-h, Diagrams showing the float arrangement in three species of *Azolla* based on the literature summarized in Table 1,  $\times 50$ . f, *A. teschiana*, g, *A. montana*, h, *A. anglica*. ac = apical cap; hc = hairy central region (suprafilosum); co = collar; e = exine; en = endoperine; ex = exoperine; i = infrafilosum.

which are indistinguishable either in actual number or in morphology, and for which no new reflected light observations are available. Those species described by Snead (1969) have already been mentioned, but in other species, e.g. *A. elegans* Jain and Hall, the floats have been lost during preservation and the preservation state itself may often obscure the float number due to compression etc. A number of other species of *Azolla* possess a large number of floats, but these are recognizable and countable entities, e.g. *A. schopfii* Dijkstra (Pl. 23, figs. 5, 6), where fifteen to twenty-two floats have been recognized. They are attached to the megaspore by a web of hairs arising in the central region. Floats enmeshed in this way are often obscured when viewed by SEM (e.g. *A. velus* in Martin 1976a). Using transmitted light, however, it is clear that the floats, although recognizable structures, are held together only loosely, being easily dislodged (Pl. 23, figs. 5, 6). Reflected light micrographs (Sweet and Chandrasekharam 1973), do reveal the floats clearly for *A. schopfii* and indicate the variability in their arrangement as suggested by transmitted light observation. This somewhat loose arrangement of the floats is further expressed in the range of morphology of the megaspore

and the float zone. *A. velus* and *A. stanleyi* (see Table 1) have a similar loose aggregation of floats.

*A. colwellensis*, however, viewed also in transmitted light for direct comparison (Pl. 23, fig. 7), has a much more compact float zone and a consequent uniformity of megaspore and float zone shape (see Pl. 23). Other species with a similar compact arrangement of many but countable floats as recorded in the literature, are summarized in Table 1 and include *A. teschiana* Flörshütz, *A. montana* (Hall and Swanson), *A. anglica* Martin, *A. bulbosa* Snead, and *A. distincta* Snead.

*A. teschiana* figured by Snead (1969) does not reveal any float pattern. Dijkstra (1961) figured a reconstruction from Flörshütz (1945) which has been vindicated by SEM observations (Martin 1976a). There are twenty-four floats of very similar sizes arranged in three tiers in a closely compact mass (text-fig. 1f). *A. bulbosa* appears to be very similar to *A. teschiana* from Snead's figure and description. *A. distincta* when studied by SEM (Hall 1974) revealed two tiers of floats, the upper tier larger than the lower. The floats in *A. montana* were originally described as surface features only, barely differentiated from the dome-shaped columella, but Martin (1976a) states in a footnote that Hall has suggested that there may be a well-defined central column in this species. If this is the case, then *A. montana* may be quite similar to *A. colwellensis*. However, Hall's (1974) SEM illustration demonstrates, as noted by Hall and Swanson (1968) and Jain and Hall (1969), that *A. montana* has only two tiers of floats, all being of similar size and not apparently arranged in three groups of six (see text-fig. 1g). In addition, the float zone is equal to, or less than, the megaspore zone in extent. *A. montana* and *A. colwellensis* are thus distinct species in this respect. *A. anglica* is most similar to *A. colwellensis* in its float zone arrangement, having up to twenty-four floats in three tiers (text-fig. 1h). The float zone, however, only occupies one-third of the entire megaspore apparatus.

Whilst it is necessary to re-examine all species previously seen only with transmitted light, before a complete assessment of multifloated *Azolla* species can be made, *A. colwellensis* appears to be distinct in its float pattern from all other recorded species. It is, however, most similar to *A. montana* and *A. anglica*.

#### *Retention of floats, and presence of cap and collar*

Two methods of float retention have been described for *Azolla* species. The first is the development of hooked maniculae from the central column (Martin 1976a), as for example in *A. anglica*, *A. velus*, and *A. teschiana*. These maniculae supposedly entangle with hairs on the floats, and Martin suggests that they will occur in all species of Section *Kremastospora*. They have not been recorded by other workers and do not occur on *A. colwellensis*.

The second method is the trapping of the floats within a domed meshwork of hairs (suprafilosum) derived from a basal collar as in *A. prisca* (Fowler, 1975). In less differentiated species, a web of hairs arises from the proximal megaspore surface and similarly enmeshes the floats, as in *A. schopfii*, but no distinct basal collar is present. The float system is thus very variable in appearance, the floats being securely attached to the megaspore, but able to shift in position with respect to it. The term loose float arrangement has been used here to describe this morphology. A very similar condition exists in Cretaceous genera similar to *Azolla*, e.g. *Azollopsis* and *Glomerisporites* (Hall, 1974).

Martin (1976a) emphasized the importance of the retention mechanism and commented that the collar occurred relatively late; in Upper Oligocene and younger species. However, Sahni (1941) recorded *A. intertrappea* (with a 'reflexed flange' possibly a collar) in the Eocene, and I here record *A. prisca* from the Eocene (Pl. 24, fig. 11), which has a very well-defined collar. Thus the collar occurs in Eocene nine- and three-floated species, and is here recorded for the first time in an Eocene multifloated species, namely *A. colwellensis*.

The existence of an apical cap has been recorded in two multifloated species—*A. montana* and *A. anglica*—but not in conjunction with a collar as in *A. colwellensis*. Martin (1976a) considered that the cap (apical membrane) along with the basal collar, constituted the retention mechanism, and felt that the hairy web was useful in retention only in conjunction with hooked maniculae. The cap, however, as part of the original megasporangial wall, may be present in all *Azolla* species; its absence being due to lack of preservation. Clearly the dome-shaped suprafilosum passing up through the

centre of the float zone and out over the apex, would act as a float retention mechanism without an apical cap. Although the cap is usually preserved on species with a basal collar, this is probably because the float zone is compact rather than because the cap is causing the compact arrangement (on *A. teschiana* for example the cap is absent). Prior to the development of a distinct collar, a diminutive collar—merely an extension of the perine—would assist in float retention, and produce a compact float arrangement. This may occur, for example, on *A. anglica* where it is noted that the distinction between the zones of the perine is lost at the megaspore apex. The fact that many specimens of *A. anglica* had lost their floats, suggests that this or the possible manuculae, were not very effective float retention mechanisms. It is the occurrence of the collar, and the associated development of a central zone within the float zone through which the suprafilosum (derived from the collar) extends up to and over the apex, which is most important in float retention. It is possible that on some species, manuculae also aided float retention, but in my opinion their presence is of little significance when compared with the above mechanism.

It has been recognized that nine- and three-floated species (with compact float arrangements) are trisepate, with the float zone divided into three compartments formed from the suprafilosum. In multifloated *A. colwellensis*, no trisepation has been observed, but the floats have been seen to occur in three distinct groups. The junction between the groups is sometimes sharp (Pl. 23, fig. 4a), and is thus very similar to the septum, as for example, in *A. prisca*. In other places, however, there is no vertical boundary between two groups of floats (Pl. 23, fig. 4c right hand edge). It does appear that, along with the development of a collar and dome-shaped suprafilosum, came a tendency towards the trisepate condition, which is so far only known to be fully developed in nine- and three-floated species.

*A. colwellensis* is the youngest recorded multifloated *Azolla* species, and is the only multifloated species with a distinct collar aiding float retention. In addition, it has a well-developed dome-shaped suprafilosum, originating from the collar, and passing upwards through the centre of the float zone, showing an arrangement of the floats in three groups with a tendency towards trisepation.

#### *Megaspore wall structure*

Snead (1969) and Kempf (1969b) have both emphasized the importance of megaspore wall structure in the classification of *Azolla* species. This feature however is not usually referred to in the diagnoses of the various sections within the genus (see Fowler 1975 and Hall and Swanson 1968), which are based on the features discussed above, and on the microspore massulae (see below). Nevertheless, the literature on detailed sporoderm architecture is increasing; Fowler and Stennett-Willson (1978) and Martin (1976a) have described Recent species, and Martin (1976a), Friis (1977), Fowler (1975), Martin (1976b), and Snead (1969) have provided detailed description and illustration of fossil forms. Earlier literature is, however, poorly illustrated, and there is considerable difficulty in comparing the many known species. Confusion exists particularly between surface and sectional based descriptions.

A three-layered sporoderm structure is characteristic of *Azolla* species comprising the exine (megaspore wall proper), the endoperine, and the exoperine. In some fossil species the detail of the surface of the megaspore exoperine is entirely obscured by a covering of hairs which are derived from the exoperine itself, forming the infrafilosum, as in *A. colwellensis* (Pl. 23, fig. 2; Pl. 24, fig. 4). *A. prisca* also possesses a hairy exoperine, but in this case the hairs are derived from particular areas (the tubercles—Pl. 24, fig. 10), and do not totally obscure the megaspore surface.

In other fossil species, for example, *A. vehus* (see Martin 1976a), a hairy covering extends only part way down the megaspore, and thins out completely at the distal face. These hairs are derived from the collar region, and are in fact part of the suprafilosum, not part of an exoperine infrafilosum. In these species the exoperine is usually visible in surface view and is variously foveolate, reticulate, rugulate, or tubercled (see *A. schopfii*, Pl. 23, figs. 5, 6). Such species include *A. teschiana* and *A. anglica* (Martin, 1976b), *A. nikitinii* (Friis, 1977), *A. ventricosa* (Friis, 1977), *A. montana* (Jain and Hall, 1969), and *A. schopfii* (Sweet and Chandrasekharam, 1973). In *A. montana* the outermost hairy zone, termed



the perispore (Hall and Swanson 1968), is very easily detached and is clearly not derived from the underlying exoperinal wall elements. The wall sculptural elements are usually clavate in sectional view and variously united along their length or at their tips, to produce the effect of a surface reticulum. In some of this group of species the hairs only extend a very short distance below the float zone, as in *A. bulbosa* and *A. barbata* (Snead, 1969).

Difficulties arise when considering a number of other species where the descriptions do not make clear whether the hairy outer layer of the megaspore is in fact derived from the collar (is suprafilosum), or derived from the exoperine (is infrafilosum). In the latter case it will not be detachable. Multifloated species where such information is lacking, include *A. distincta*, *A. filosa*, *A. lauta*, *A. pilata*, *A. fistulosa*, and *A. conspicua* of Snead (1969), and *A. fragilis*, *A. elegans*, and *A. stanleyi* of Jain and Hall (1969). Of these species *A. fragilis* (together with *A. extincta* of Jain 1971) is considered synonymous with *A. schopffii* (Sweet and Chandrasekharam, 1973). *A. fistulosa* is considered by Jain (1971) to be synonymous with *A. distincta*, and is shown to have 'an often lost' (i.e. detachable) hairy layer, derived from the suprafilosum. *A. pilata* was transferred to *Savinia* by Jain (1971).

The thickness of the wall, ranging from 26 to 145  $\mu\text{m}$  in the remaining multifloated species where the origin of the hairy layer is uncertain, prevents their being closely comparable with *A. colwellensis*. None of the previously figured sections of sporoderm is exactly comparable with that of *A. colwellensis*; the elements of the inner zone of the exoperine are usually predominantly clavate beyond a thin columnar zone (Fowler 1975, text-fig. 1c; Martin 1976b, text-fig. 1a). *A. colwellensis*, however, has no defined columnar zone, and has coalescing rugulae rather than a clavate structure (Pl. 24, fig. 3; text-fig. 1b).

Although it has not been possible to make a fully detailed comparison, it seems clear that the sporoderm of *A. colwellensis* is distinct from that of all other fossil species with a similar megaspore apparatus. In the possession of the exoperinal hairs, the species is similar to *A. prisca*, but otherwise the two species are very different. Those species with the most similar float arrangement—*A. anglica*, *A. montana*, and *A. schopffii*—do not possess hairs arising from the exoperine.

#### *Microspore massulae*

Features of the microspore massulae of *Azolla* species are summarized in Table 1. Anchor-shaped glochidia with a distal dilation (gad on Table 1) occur throughout the range of the genus on both multi-, nine- and three-floated forms. They occur on species with a single columellate float, for example in *A. simplex* and *A. primaeva*, on three-floated *A. indica* and *A. intertrappea*, on nine-floated *A. prisca*, and on multifloated *A. montana* and *A. anglica* (which are considered most similar to *A. colwellensis* in float arrangement), all in pre-Oligocene strata. Their occurrence is probably related to the possession of hairs on the megaspore surface, to which the anchor-shaped tips can become attached or enmeshed. Whether these hairs are derived from the suprafilosum, and occur around the collar only, or are derived from the exoperine (infrafilosum) and occur all over the megaspore, may be of very little significance for massula attachment. It is possible that the possession of a hairy protruding collar (an area where hairs of both types may become intertwined), results in the attachment of many massulae in that area, nearest to the proximal megaspore face, as is often the case in *A. prisca* (Pl. 24, fig. 10).

Anchor-shaped glochidia with a distal dilation which are also septate, occur only in *A. colwellensis* and *A. anglica* among multifloated species. They also occur in the Eocene *A. intertrappea* and in two modern species. Godfrey *et al.* (1961) recorded both septate and non-septate glochidia on the same massula in *A. caroliniana*. It is therefore probably unwise to assign any particular significance to the presence of septae. Also, as Fowler (1975) suggests, the junction between the solid head of the glochidium and the hollow stalk may in some cases have been misinterpreted as a septum.

TABLE 1.

Species	References	Veg.	Megaspores	Massulae	Age
<i>Azolla simplex</i>	Hall 1969b		Ic	gad	Lower Cretaceous
<i>A. barbata</i>	Snead 1969 Hall and Bergad 1971 Hall 1974		(N) ii	+gch	Cretaceous- Palaeocene
<i>A. extincta</i>	Jain 1971 (= <i>A. schopfi</i> , see Sweet and Chandrasekharan 1973)		(N)	+eg	Cretaceous
<i>A. genesiana</i>	Hills and Weiner 1965 Hall and Swanson 1968 Srivastava 1968		3/lc	ga	Cretaceous
<i>A. cretacea</i>	Stanley 1965 Srivastava 1968 Hall 1974 Srivastava 1975		? as <i>A. montana</i> Jain and Hall, 1969 or unknown	gad	*? Cretaceous, Palaeocene, and Lower Eocene
<i>A. circinata</i>	Oltz and Hall in Hall 1968			gch	Cretaceous
<i>A. gigantea</i>	Bergad and Hall 1971			gad	Cretaceous
<i>A. sagittifera</i>	Srivastava 1968			gab	Cretaceous
<i>A. hamata</i>	Srivastava 1968			gch	Cretaceous
<i>A. pilata</i>	Snead 1969 (transferred to <i>Salvinia</i> in Jain 1971)		floats lost		Cretaceous
<i>A. conspicua</i>	Snead 1969		(N)		Cretaceous
<i>A. lauta</i>	Snead 1969		(N)		Cretaceous and Palaeocene
<i>A. fistulosa</i>	Snead 1969 (= <i>A. distincta</i> Jain, 1971)		(N)		Cretaceous and Palaeocene
<i>A. filosa</i>	Snead 1969		(N)		Cretaceous and Palaeocene
<i>A. distincta</i>	Snead 1969 Hall and Bergad 1971 Hall 1974 Jain 1971		N: ? 15 ii/iii	+ga	Cretaceous and Palaeocene
<i>A. schopfi</i>	Dijkstra 1961 Snead 1969 Sweet and Chandrasekharan 1973	veg	15-18 ii/iii 15-22 iii	ga gch/simple	Cretaceous and Palaeocene
<i>A. montana</i>	Hall and Swanson 1968 emend. Jain and Hall 1969 Hall 1974		10/15-20 ii	+gad	Cretaceous, Palaeocene, and Lower Eocene
<i>A. bulbosa</i>	Snead 1969		18 iii		Palaeocene
<i>A. fragilis</i>	Jain and Hall 1969 (= <i>A. schopfi</i> Sweet and Chandrasekharan 1973)		(N)		Palaeocene
<i>A. elegans</i>	Jain and Hall 1969		floats lost		Palaeocene
<i>A. stanleyi</i>	Jain and Hall 1969		15-N	+ga	Palaeocene
<i>A. velus</i>	Dijkstra 1961 Jain and Hall 1969 nov. comb.		10-N ii	+ga	Palaeocene
<i>A. teschiana</i>	Martin 1976a Flörschutz 1945 Dijkstra 1961 Martin 1976a		24 iii	+ga	Palaeocene
<i>A. anglica</i>	Martin 1976b		up to 24 iii	? +gads	Palaeocene
<i>A. berryi</i>	Brown 1934	veg			Middle Eocene

TABLE 1 (cont.)

Species	References	Veg.	Megaspores	Massulae	Age
<i>A. intertrappea</i>	Sahni and Rao 1943 (Sahni 1941) Hall 1969a	veg	3	+gad	Eocene
<i>A. indica</i>	Trivedi and Verma 1971		3	gads	Lower Eocene
<i>A. primaeva</i>	Arnold 1955 Hills and Weiner 1965 Hills and Gopal 1967 Hall 1969a	veg	1c	gad	Eocene
<i>A. antiqua</i>	Dorofeev 1959a		t 6-9 ii		Upper Eocene-Lower Oligocene
<i>A. colwellensis</i>	This work		18(-24) iii	+gads	Upper Eocene
<i>A. prisca</i>	Reid and Chandler 1926 emend. Fowler 1975	veg	t 9 ii	+gad	Upper Eocene-Lower Oligocene
<i>A. suchorukovii</i>	This work Dorofeev 1968b		t 9 ii		Oligocene
<i>A. nana</i>	Dorofeev 1959a		t 9 ii	eg	Oligocene
<i>A. turgaica</i>	Dorofeev 1959a		t 9 ii	eg	Oligocene
<i>A. sibirica</i>	Dorofeev 1959a, 1962, 1963		t 9 ii		Middle Oligocene
<i>A. parapinnata</i>	Dorofeev 1962, 1963		t 9 ii		Oligocene
<i>A. ventricosa</i>	Nikitin 1948 Dorofeev 1959a, b, 1962, 1963 Nikitin 1965 Friis 1977 (First formal diagnosis in Dorofeev 1959b)		t 9 ii	eg	Oligocene-Miocene
<i>A. vera</i>	Kryshstofovitch 1952	veg			Oligocene
<i>A. bohémica</i>	Pactova 1958			gad	Upper Oligocene-Lower Miocene
<i>A. nikitinii</i>	Dorofeev 1955a, b, 1959b Lancucka-Srodniowa 1958 Dorofeev 1962, 1963 Friis 1977		t 9-12 ii		Upper Oligocene and Miocene
<i>A. tertiara</i>	Berry 1927	veg			? Miocene/Pliocene
<i>A. tuganensis</i>	Dorofeev 1962, 1963 Friis 1977		t 3 i	+ga	Upper Oligocene and Miocene
<i>A. glabra</i>	Nikitin cited in Dorofeev 1955a, c, 1959b Lancucka-Srodniowa 1958		3 i	gas	Upper Oligocene and Miocene
<i>A. tomentosa</i>	Nikitin 1948 Dorofeev 1959b, 1962, 1963 Bertelsen 1974		3 i	+gas	Upper Oligocene and Miocene
<i>A. aspera</i>	Dorofeev 1963		t 9-12 ii	+eg	Upper Oligocene and Miocene
<i>A. sulaensis</i>	Dorofeev 1968a		t 9 ii		Middle Miocene
<i>A. parvula</i>	Dorofeev 1968a		t 9 ii		Upper Miocene
<i>A. pulchella</i>	Dorofeev 1969		t 9 ii		Upper Miocene
<i>A. ucrainica</i>	Dorofeev 1968a		3 i	ga	Upper Miocene
<i>A. roemoeensis</i>	Bertelsen 1974		t 9 ii		? Upper Miocene
<i>A. pseudopinnata</i>	Nikitin 1957 Lancucka-Srodniowa 1958 Dorofeev 1959a, b, 1963		t 9 ii		Upper Miocene-Lower Pliocene
<i>A. pyrenaica</i>	Flörschutz and Amor 1960 Potoniè 1962		3 i	ga	Upper Pliocene and Pleistocene

TABLE I (cont.)

Species	References	Veg.	Megaspores	Massulae	Age
<i>A. tegeliensis</i>	Flörschutz 1938 emend. Bertelsen 1972 Potonié 1962 Kempf 1969a		t 9 ii	? <i>A. danica</i>	Upper Miocene, Pliocene and Pleistocene
<i>A. danica</i>	Bertelsen 1972			g simple, hair-like, bifurcating occa- sionally	Lower Pleistocene
<i>A. interglacialica</i>	†Nikitin 1957 Dorofeev 1956 Kolesnikova 1964		3 i	+gads	Pliocene and Pleistocene
<i>A. filiculoides</i> Lam.	Madler 1954 Godwin 1975 Martin 1976a Fowler and Stennett- Willson 1978 Pieterse <i>et al.</i> 1977	veg	3 i	+gads	Upper Pleistocene and Recent
<i>A. microphylla</i> Kaufuss	Svenson 1944 Fowler and Stennett- Willson 1978	veg	3 i	+gs	Recent
<i>A. caroliniana</i> Willd.	Strauss 1952 ‡Martin 1976a Svenson 1944 Godfrey <i>et al.</i> 1961 Pieterse <i>et al.</i> 1977	veg	3 i	+gads	Upper Pleistocene and Recent
<i>A. mexicana</i> Presl.	Svenson 1944	veg	3 i	+gs	Recent
<i>A. nilotica</i> Decaisne	Martin 1976a Fowler and Stennett- Willson 1978	veg	9 ii	+eg	Recent
<i>A. pinnata</i> R. Brown including <i>A. im- bricata</i> (Rox- burgh) Nakai	Sweet and Hills 1971 Martin 1976a Fowler and Stennett- Willson 1978	veg	9 ii	+g straight unhooked	Recent

\* *A-olla cretacea* is extended into the Eocene if accepted as belonging to *A. montana*. Jain and Hall (1969), however, suggested the retention of the separate name *A. cretacea* for isolated massulae of this type.

† *A. interglacialica* Nikitin, 1957 is considered by Lancucka-Srodniowa (1958) to be identical with *A. filiculoides*.

‡ Keith Fowler (pers. comm. 1978) believes that Martin (1976a) examined megaspores of *A. microphylla* in mistake for *A. caroliniana*.

#### Explanation to the abbreviations:

Veg.: Indicates that vegetative material is known.

References: The first reference indicates the author of a fossil species.

Megaspores: Number of floats: ( ) = indistinct; N = Numerous. Float characters: t = trisepate; c = columellate. Float numbers: Arabic figures. Number of float tiers: Roman figures.

Massulae: + = massula recorded attached to megaspore; eg = eglochidiate; ga = glochidia anchor-shaped; gad = glochidia anchor-shaped with a distal dilation; ch = glochidia coiled and hair-like; b = barbed; s = septate.

## DISCUSSION AND PHYLOGENETIC IMPLICATIONS

The previous section has demonstrated the differences between *A. colwellensis* and those species which are of a similar morphology, or occur at a close stratigraphic horizon. The data are summarized in Table I where it may be seen that a similar combination of features occurs only in *A. anglica* and *A. montana*. In the latter the floats are shown to be usually in two tiers (Hall 1974), their number being very irregular; the float zone occupying less than half, usually one-third, of the megaspore apparatus, and the float arrangement, although compact, is very variable, as is the

megaspore apparatus shape. The glochidia are shorter than those of *A. cobwellensis* and are non-septate. *A. anglica* has a float zone very similar in float number and arrangement to that of *A. cobwellensis*; however, the float zone usually occupies only about one-third of the megaspore apparatus. The glochidia are shorter and are very narrow for half their length, expanding to a broader end with a weak distal dilation. Neither *A. montana* nor *A. anglica* possesses a hairy perispore arising from the exoperine, or a collar delimiting the base of the float zone.

The existence of *A. cobwellensis* as a distinct species of *Azolla* is therefore established. It is similar to the species mentioned above and also to *A. schopfii*, *A. teschiana*, *A. velus*, and *A. distincta*. Of these, *A. velus* and some specimens of *A. distincta*, have floats in two tiers, the upper larger than the lower, whilst the other species have floats in three tiers. In *A. teschiana* (text-fig. 1f), all the floats are of a similar size, and so it may be suggested that this species represents the least differentiated multifloated form.

It has been demonstrated by Martin (1976a) that the floats of *Azolla* are derived from aborted megaspores. His summary of the life cycle shows that thirty-two potential megaspores are produced and thirty-one abort. He has also demonstrated the presence of immature megaspores in the perine of the mature megaspore, and also in the pseudovacuolate floats. He suggested that if twenty-four floats are the result of extension of the tissue of twenty-four aborted megaspores, then a further seven aborted megaspores must be embedded in the tissue of the mature megaspore perine, though these actual figures have yet to be proven. Such a hypothesis separates the megaspores into four sets of eight, with three sets forming the floats. Twenty-four floats, one per aborted megaspore, would thus be the maximum, and it is interesting to note that not more than twenty-four floats (but up to twenty-four in three cases) have been recorded. Further, it seems likely that the so-called septation of floats into a smaller one and a larger one is merely the reduction in size of one float, prior to a condition where it will have merged with the larger float. However, the record of ripetisation of all of the twenty-four floats in *A. teschiana* (Hills and Gopal, 1967, p. 1088) is not in harmony with this view. Nevertheless, it seems plausible to accept twenty-four as the basic float number in *Azolla* species. By the merging of various floats it is possible to derive any of the smaller numbers from this figure.

The occurrence of the floats in two or three tiers need not be of any particular phylogenetic significance, as even in those species with a compact float arrangement, the positioning of the floats will be partly controlled by the space available in the float zone. Also, the upper tier of floats will by this reasoning tend to be larger than the lower tier. The upper tiers may well contain a higher number of aborted megaspores.

The presence of three- and one-floated forms in the same stratigraphic levels as the many-floated forms, shows that it is not certain that they are derived from the latter by reduction in float number. It has, however, been suggested (Jain 1971) that all these early three- and one-floated species (see Table 1) may need reinterpretation, due to lack of previous detailed study, and difficulties in observation of certain preservation states. Accepting their existence, however, indicates that all the abortive megaspores became aggregated into one or three groups in some species, at an early stage in the evolution of the genus. These species would probably then represent a different lineage from the multifloated species, and it is possible that four lineages may be recognized with one, three, nine, and more than nine floats, as suggested by Hall (1969) and Martin (1976a).

Previous authors have attributed considerable significance to the fifteen floats of *A. schopfii*, but this has now been shown to have up to twenty-two floats (Sweet and Chandrasekharam 1973). It is very important in future studies of multifloated *Azolla*, that the basic float number should be recognized, for example eighteen in *A. cobwellensis*. All the multifloated species except *A. teschiana*, may have a basic number of eighteen, but in *A. anglica* it could be twenty-four, and in *A. montana*, *A. distincta*, *A. stanleyi*, *A. schopfii*, and *A. anglica* it could be fifteen. In more recent species, distinct records of nine- and three-floated forms occur, but still examples of six and twelve floats are known. Thus a series of 24, 18, 15, 12, 9, 6, 3, 1, floats is known, which lacks only one unit (twenty-one floats which could easily be the number for one of the species not well studied), to include all the permutations of the successive merging of one further abortive megaspore, in each part of the

three-partite float zone. Similarly, the most reliable records 24, 18, 9, and 3, represent the merging of two abortive megaspores in each part of the float zone.

The variation in float number in *Azolla* species could therefore be due to the variation in the grouping of twenty-four of the abortive megaspores within the float zone. Species occur with one abortive megaspore per float, each float being of similar size. Other species, for example those with eighteen floats, have the upper tier of floats larger, perhaps each containing three abortive megaspores, with one each in the lower floats. Three-floated forms may have eight abortive megaspores to each float. That these morphologies have arisen in any particular sequence is not substantiated by the fossil record, which actually indicates that there may have been a number of separate lineages, species from each existing contemporaneously.

That the merging of the abortive megaspores into groups within the floats is a very 'plastic' feature is substantiated by the range of float numbers recorded for some species (Table 1). During this study, one specimen of *A. prisca* (Pl. 24, fig. 12), collected from the Bembridge Marls, was found to have two floats at the positions of each float in the lower tier, giving a total of fifteen floats.

Apart from the attempt to elucidate *Azolla* phylogeny in terms of variation of float numbers, variation in glochidia morphology has also been used. Mahabale (1963) suggested that a reduction had occurred in glochidia form, assuming that septate glochidia with anchor-shaped tips were primitive and reduced through three stages: the first non-septate with anchor-shaped tips; the second not anchor-shaped, merely hair-like; and the third missing altogether. Jain (1971) objected to this hypothesis on the basis that all these features could be found in Cretaceous *Azolla* and related genera. The data on Table 1 support this claim, and show that there is no distinct change of trend in glochidia morphology supported by the fossil record. The glochidia morphology is to some extent adapted to the megaspore structure; those with anchor-shaped tips being ideal for trapping on the hairy megaspore surface. However, this hairy surface may be derived from the megaspore exoperine or from the collar region, so it does not necessarily indicate a close phylogenetic relationship for all species with anchor-shaped glochidia.

The seven sections now recognized within the genus *Azolla* (see Fowler 1975, pp. 486, 488), are defined on the above parameters, i.e. float number and glochidia morphology. Apart from *A. barbata* (section Filifera), all multifloated species have anchor-shaped glochidia (section Kremastospora). Other anchor-shaped glochidia are found in sections *Azolla* and Trisepta, which have three and nine floats respectively.

Very little emphasis has been placed on megaspore wall structure in classification, although recent studies (Martin 1976a, b and Fowler and Stennett-Willson 1978) have paid more attention to this feature. It is still not clear how the wall structure may have been derived, and the present study has shown no trend in the stratigraphic occurrence of particular morphologies, nor any particular wall morphology consistently associated with a particular float number etc. More work is needed before the megaspore wall structure can be successfully used in phylogenetic interpretations.

The presence of a collar on a multifloated species is a new occurrence. This could, however, be interpreted in two ways: first, that multifloated forms with a collar gave rise to three- and nine-floated forms (also with a collar); and secondly, the collar may have arisen in three separate instances in multifloated, nine- and three-floated species.

Clearly, despite the extensive fossil record of *Azolla*, no clear idea of the evolutionary development within the genus is yet available. One major feature of note is that multifloated species became extinct by the end of the Eocene. However, two features previously known only in species with a small float number, namely the presence of a collar and a tendency towards a triseptate float zone, have now been shown to occur in an Eocene multifloated species. In a genus where five of the sections and nearly 90% of the species are fossil, and certain major variations in morphology (e.g. numerous floats) are known only from fossil species, the importance of the fossil record is self-evident. Within this record there are two important steps needed to extend our knowledge: the first is a reinvestigation of certain poorly described multifloated species, and the second an unequivocal answer to the controversy concerning the number of floats on the species *A. simplex*, *A. genesiana*, and *A. primaeva* (section Simplicispora).

## CONCLUSIONS

Specimens of *Azolla* with numerous floats fall into one of four categories: 1, floats indistinguishable; 2, floats enmeshed loosely in a hairy weft, and thus able to shift their position with respect to the megaspore; 3, floats enmeshed in a hairy weft derived from a basal collar, thus forming a compact structure; and 4, floats in a compact structure held together by maniculae on the floats. This latter situation, described by Martin (1976a, b) has not been observed by other workers, and it seems possible that at least one species supposed to possess this feature may in fact have a diminutive collar. *A. montana* has a compact float arrangement (but no collar or maniculae), and this may be due to the development of a well-defined dome-shaped hair weft, as occurs in those species which do have a collar. *A. cobwellensis* is the only species in category three above, and as such it may be considered one of the most adapted of the multifloated species. In addition, it is the only multifloated species with a tendency to trispertation of the float zone, and with a hairy exoperine. It is also the youngest multifloated species yet recorded.

Evidence of plasticity in float number in *Azolla* is afforded by the variation in float number in *A. cobwellensis*, and by a specimen of *A. prisca* (usually with nine floats) with fifteen floats. It is concluded that float number is dependent on the number of abortive megaspores which are merged within each float. A theoretical maximum of twenty-four floats (one megaspore to each float), requires that seven abortive megaspores should be embedded in the perine of the mature megaspore. Any number of floats may occur, depending on the number of megaspores in each. No one float number need be derived from another number, but each may occur as an independent variation on this basic theme.

Megaspore wall structure, while emerging as a useful specific feature, is not yet well enough studied to be used in phylogenetic interpretations. Microspore massulae with anchor-shaped glochidia occur throughout the range of the genus, on multifloated, nine-, three-, and one-floated species. Their presence is probably related to the possession of a hairy megaspore surface in which they become entwined. As such a surface may be derived from two different parts of the megaspore apparatus, species with anchor-shaped glochidia need not be closely related. The significance of the presence of septae in the glochidia is not clear, *A. cobwellensis* and *A. anglica* being the only multifloated species which possesses them.

The significance of *A. cobwellensis* lies in demonstrating that a number of features previously known only from nine-, three-, or one-floated species, are now recorded in a multifloated species. This is also the youngest multifloated species known, being of Upper Eocene age. This new record may be seen as adding to the complexity of the record of the genus and supporting ideas that many different lineages may have been involved in the evolution of the genus *Azolla*.

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MARGARET E. COLLINSON

Palaeontology Department  
British Museum (Natural History)  
Cromwell Road  
London SW7 5BD

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